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LEAF-BASE PHYLLODES AMONG THE LILIACEAE¹

AGNES ARBER

(WITH FOUR FIGURES)

In a recent paper (1) the writer advocated the view that leaves of monocotyledons have no true laminae, but are either equivalent to petioles+leaf-bases, or are still further reduced until they reach the point of representing leaf-bases alone. In the paper cited, attention was mainly concentrated upon petiolar phyllodes, but in the present article it is proposed to review certain leaves among the Liliaceae which seem to be of leaf-base or leaf-sheath nature, and to consider the evidence upon which this interpretation is based.

There are a number of leaves among different tribes of the Liliaceae whose external appearance and general structure may well be taken to suggest a leaf-base origin. They show no differentiation into sheath and limb; they are parallel veined and furnished with a single series of normally orientated bundles. As examples Hemerocallis, Tulipa, and Scilla may be cited. view which presupposes a considerable power of development on the part of the leaf-sheath is not necessarily too extreme, is indicated by the fact that in some monocotyledons, in which there is a differentiation into sheath and limb, the sheaths may attain remarkable dimensions. For instance, the sheath of Typha may be half a meter long (3). Again, Domin's (2) researches among the Umbelliferae have revealed a case in which all the foliage leaves are undoubtedly of leaf-base nature, namely, Oreomyrrhis linearis Hemsley. The linear leaves of this species, which bear a general resemblance to those of monocotyledons, terminate in a small rudiment apparently representing the blade.

There is not, in fact, any a priori difficulty in the way of interpreting the leaves of Tulipa, etc., as leaf-base phyllodes. We may now consider what positive evidence can be adduced in favor of this theory.

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Ontogenetic evidence

Hemerocallis fulva L.—An apical bud of this plant was dissected on March 1. Neither in a leaf about 1 mm. long viewed under the simple microscope, nor in younger leaves examined with the compound microscope, could any distinction be discerned between the "leaf-sheath" and the rest of the leaf. The leaf is open to the extreme base, so that no closed sheath is formed.

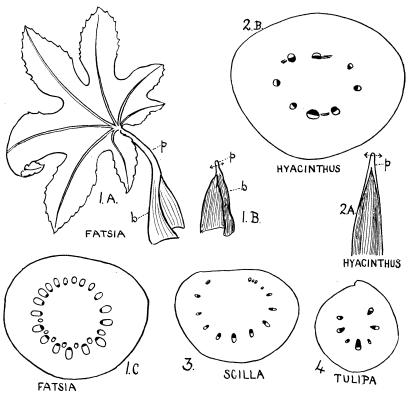
Scilla hispanica Mill.—The young foliage leaves for the current year were examined on March 1. All the leaves, down to the youngest, were found to be similar structures, in which the hooding of the apex was a relatively more conspicuous feature than in the older leaves. In the mature leaf, the sheath is seen to be closed for a very short distance at the base.

The conclusion to be drawn from the development of the leaves of these two species seems to be that in the case of *Hemerocallis* there is no evidence from the ontogeny of the existence in the leaf of any region except the leaf-base or leaf-sheath; in *Scilla* the main part of the leaf seems also to be of leaf-base nature, although the apical region of the hooded tip may possibly bear another interpretation, to which reference will be made later.

Evidence of comparative morphology

In order to test the interpretation here suggested, which explains the leaves of Tulipa, etc., as essentially leaf-base members, a search was made for some dicotyledon possessing both leaves with a well differentiated leaf-base, petiole, and lamina, and also reduced leaves which could be closely compared with those of the monocotyledons in question. Such a plant was found in $Fatsia\ ja\ ponica$ Decne., of the Araliaceae, often cultivated under the name of Aralia. The normal foliage leaves of this plant are shown in fig. 1 A. There is a well marked sheathing leaf-base (b), a petiole (p), and a palmate lamina. In addition, there are transitional leaf forms with reduced blades, culminating in bladeless bud-scales (fig. 1 B). These are of the same nature as the leaf-base of the normal leaf, although they are thinner in texture, and the parallel veining is more obvious. The most interesting feature, however, is that the apical region of the bud-scale, which is developed in

varying degrees, is solid and approximately cylindrical, and may be interpreted as the rudiment of the leaf-stalk (fig. 1B, p). The



Figs. 1–4.—Fig. 1, Fatsia japonica Decne.: A, small normal foliage leaf; b, leaf-base; p, petiole; B, bud-scale; b, leaf-base; p, rudiment of petiole; C, transverse section of apex of bud-scale at position marked with arrow in B; A and B, half natural size; C, $\times 23$; fig. 2, Hyacinthus (garden var.): A, apex of leaf (half natural size); B, transverse section through apex of leaf shown in A, at level of arrow; $\times 23$; fig. 3, Scilla (garden var.): transverse section through apex of leaf which was flat and dorsiventral except at tip; $\times 14$; fig. 4, Tulipa sylvestris: transverse section through apex of leaf which was flat and dorsiventral except at tip; form on upper side shows first indication of opening into main flat part of leaf; $\times 23$.

transverse section of this region shows a slightly dorsiventral ring of bundles (fig. iC), so that the anatomy is distinctly petiolar.

When we turn to the monocotyledonous leaves which we wish to interpret, we find that in certain of them there is an apical structure which closely parallels the petiole rudiment of the bud-scales of Fatsia. In the garden hyacinth, for instance, the leaves may often be found to terminate in a short, solid, cylindrical apex (fig. 2A). On cutting sections of this apex, a ring of bundles is revealed (fig. 2B), so that not only the external appearance of the apex but also its anatomy corresponds to that of the Fatsia bud-scales. Precisely the same thing has been found in another of the Scilleae, a garden variety of Scilla; the transverse section of the apex of this leaf is shown in fig. 3. In a second subtribe of the Lilioideae, the Tulipeae, a conspicuously developed, solid apex may be observed, for instance, in the leaf of Tulipa sylvestris L. Sections of this apical region again reveal a typically petiolar structure. Fig. 4 is drawn from a section at the base of the apical region, and shows, in its form, the last traces of the influence of the limb, but higher up this irregularity disappears, and the apex becomes approximately cylindrical.

Such leaves as those of *Hemerocallis*, on the other hand, perhaps may be compared with the countless dicotyledonous bud-scales in which reduction has been carried still farther than in *Fatsia*, so that they retain no vestige of any part of the leaf except the sheathing base.

Summary

It is shown on evidence of ontogeny and comparative morphology that certain leaves among the Liliaceae, such as those of *Hemerocallis* and *Scilla*, are to be interpreted as equivalent to leaf-bases. The lamina is entirely absent, and the petiole is either also absent or is present in an extremely reduced form. The solid, approximately cylindrical apices in which the leaves of *Hyacinthus*, *Tulipa*, etc., sometimes terminate, are held to represent the last rudimentary phase of the vanishing petiole.

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